A BRACHYOPID LABYRINTHODONT FROM THE LOWER TRIAS OF QUEENSLAND

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(Plates xiv, xv)

Synopsis

The skull of a new species of brachyopid labyrinthodont from the Lower Triassic Rewan Formation of Queensland is described and compared with other brachyopids using the method of Welles and Estes (1969). It is the most complete and the best ossified brachyopid yet found and is closely related to a form from the Mangali Beds of Central India.

Introduction

Following an initial productive field trip to the Lower Triassic Rewan Formation in 1969 (Bartholomai and Howie, 1970 ; Howie, in press), a second trip was organized in June, 1970. The purpose of this was first to collect from known vertebrate-bearing localities, and second to explore likely areas of the Bowen Basin for further Rewan exposures. The trip was a success on both counts, yielding an excellent capitosaur skull (an account of which is almost ready for publication), several small reptile skulls similar to those reported by Bartholomai and Howie (1970), a tiny (2 cm.) temnospondylous labyrinthodont skull, and many fragmentary fish, amphibian and reptilian remains from the chief known locality (Queensland Museum field locality L78), and providing us with a new productive locality some 79 miles north-north-east from L78.

Field Locality

The new locality (A. A. Howie Field Locality Q6) is at the headwaters of Duckworth Creek, south-west of the settlement of Bluff, and lies on the north-west edge of the Mimosa Syncline. Here faces of the rarely exposed Rewan Formation are found beneath the more massive escarpments of the Middle Triassic Clematis Sandstone and the overlying Lower Jurassic Precipice Sandstone which form the northern edges of the Blackdown Tableland. Malone, Olgers and Kirkegaard (1969) note that in this area the Rewan sediments are so similar lithologically and in stratigraphic position to the Rewan Formation of the type area (which is near locality L78) that direct correlation is justified and add that they are almost certainly continuous below the surface.

This Duckworth Creek exposure consists of several small linked erosion gullies, and specimens are found in these and in the alluvium at their bases. Rewan mudstone was exposed to a maximum depth of about 20 feet and included a single broad pale green band of very fine-grained sandstone.

Associated Material

Associated with the brachyopid labyrinthodont described below were several other amphibian species but no fish or reptiles, a strong contrast with locality L78, where reptiles were a common component of the fauna. Laby-

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rinthodont remains include a femur which probably belonged to a very large capitosaur, left and right femora and other postcranial remains of a more terrestrial type of labyrinthodont, nodules containing rhachitomous vertebrae, bone scraps bearing ornament of the type described by Cosgriff (1965) in *Deltasaurus kimberleyensis*, numerous coprolites, and fragments of an unprepared skull which I think can be assigned to *Rewana* sp. (Howie, in press). Although the brachyopid skull was found in the red mudstone, all the other more complete remains came preserved in nodules from the pale green band.

The Family Brachyopidae

In 1956 Watson published a review of the brachyopid labyrinthodonts and was followed by Cosgriff (1969), who largely used Watson's criteria for inclusion of a species within the Family Brachyopidae, and Welles and Estes (1969), who built on studies of Watson, Shishkin (1964, 1966) and Bystrow (1935) to establish a revised and extended set of brachyopid characters.

Within the "brachyopids proper" Watson recognized *Bothriceps australis* and *B. major* (which he renamed *Trucheosaurus*), *Brachyops laticeps*, *Batrachosuchus watsoni* and *B. browni*, *Pelorocephalus*, and "*Platyceps*" *wilkinsoni*, but he included forms such as *Eobrachyops*, *Dvinosaurus* and the plagiosaurs within a larger brachyopid grouping. Panchen showed in 1959 that the plagiosaurs were not closely allied to the brachyopids. Cosgriff made "*Platyceps*" *wilkinsoni* the type of a new genus, *Blinasaurus* which had two known species, *B. wilkinsoni* and *B. henwoodi*, and recognized *Bothriceps*, *Trucheosaurus*, *Brachyops laticeps*, *Batrachosuchus watsoni*, *B. browni*, *Hadrokkosaurus* and *Boreosaurus* as being true members of the Family Brachyopidae. Welles and Estes took a more conservative viewpoint, eliminated genera which they thought were doubtful (*Boreosaurus*, for example) and ended with *Blinasaurus henwoodi*, *Bothriceps* (which included *B. australis*, Watson's *Trucheosaurus major* and "*Platyceps*" *wilkinsoni*, Cosgriff's type for *Blinasaurus*), *Batrachosuchus watsoni*, *B. browni* and *B. lacer* (from Sushkin's *Batrachosuchoides lacer*), *Brachyops* and *Hadrokkosaurus*, thus reducing the number of brachyopid genera to five.

I intend to follow Welles and Estes' grouping of the brachyopids and their set of brachyopid skull characters, while adding to these Cosgriff's characters for brachyopid lower jaws. I do not agree with Cosgriff's brachyopid skull character of palatal teeth being present only on the vomer bones; irregular palatine teeth can be seen in *Hadrokkosaurus* (on the ectopterygoid and palatine bones) and in *Brachyops allos* n. sp. (on the ectopterygoid bone).

Systematic Description

Class Amphibia
Subclass Labyrinthodontia
Order Temnospondyli
Superfamily Brachyopoidea
Family Brachyopidae

Characters of the family. Skull short, broad; no zones of intensive growth (other than in the cheek region—see below). Orbits anterior and usually relatively large. Otic notch absent, or at most a shallow embayment. Tabulars short and broad; tabular horns absent or weak. Parasphenoid flat, becoming elevated anteriorly above vomers. Usually a single tusk pit pair on vomer, palatine, and ectopterygoid; interstitial smaller teeth little developed or absent; tusks usually much elongated and massive; dentary tooth row relatively short. Vomerine plate short. Occiput with strong slope posteroventrally to occipital condyles, the latter usually quite large. Quadrate condyles large, ventrally produced, anteroventral in position relative to occipital condyles. Squamosal and quadratojugal with strong occipital flanges forming a vertical transversely

concave trough lateral to the pterygoid. Pterygoid forming a steeply arched, flat-roofed palate. Quadrate somewhat compressed laterally, wedged antero-laterally between flange of pterygoid and squamosal-quadratojugal trough. Retroarticular process elongate. Posterior meckelian foramen and angular-prearticular suture on ventral surface or very low on lingual surface.

Brachyops Owen 1855

Type species : *Brachyops laticeps* Owen. *Brachyops* is the first described and thus the typical brachyopid. Other brachyopids differ from *Brachyops* mainly in their skull proportions—the most obvious differences are as follows :

Blinasaurus Cosgriff (1969) differs in that its snout is more rounded, its orbits are larger and therefore closer together, its external nostrils are closer together, its parietal foramen is relatively much closer to its orbits, its tabulars and postparietals are reduced, its interpterygoid vacuities are much longer relative to their width, so that the anterior part of the palate is shortened and the posterior part lengthened.

Bothriceps Huxley (1859) has a much narrower skull so that its orbits and nares are closer together, and its interpterygoid vacuities are longer relative to their width.

Hadrokkosaurus Welles (1957) is larger than *Brachyops*, its skull is much broader relative to its length and is shorter postorbitally.

Batrachosuchus Broom (1903) has a broader, less pointed skull, the preorbital skull is shorter, the interpterygoid vacuities are longer relative to their width, and the anterior part of the palate is shortened.

Brachyops allos n.sp.

Holotype. A skull complete but for the left cheek region, part of the right quadratojugal and pterygoid, and a few scraps from the dermal skull roof. Queensland Museum No. F6572.

Type locality. A. A. Howie field locality Q6, near the headwaters of the Duckworth Creek, south-west of the settlement of Bluff, South Central Queensland.

Horizon. Lower Upper Rewan Formation of the Mimosa Group, Lower Trias.

Characters of the species. Brachyops allos differs from *Brachyops laticeps*, especially in that its exoccipital condyles are much nearer the level of the quadrate condyles, so that the backwardly sloping portion of the occiput in *B. allos* is greatly reduced. Although this character is one which Watson (1956) considered showed the stage of evolutionary advancement of a brachyopid, the two species are otherwise so alike that generic separation at this stage would be foolish. The cultriform process of the parasphenoid in *B. allos* is clasped laterally by posteriorly directed processes of the vomers rather than overlying these as it does in *B. laticeps*. Posteromedially the process bears an area of dermal denticles in *B. allos*. On the dorsal surface of the skull the tabulars are exposed a little less in *B. allos* than they are in *B. laticeps*. Anteriorly the interpterygoid vacuities are broader in *B. allos*, but this difference is less between *B. allos* and *B. laticeps* than between *B. allos* and all other brachyopids. The rather long tripartite anterior palatal foramen in *B. allos* is also distinctive.

The Skull of *Brachyops allos*

When found, the skull was lying upside down with the anterior part of the palate exposed. Although a large area was excavated when the skull was being encased in a plaster cast, no postcranial material which could positively be associated with the skull was recovered. In the laboratory exposed bones were

glued together with Butvar B76 and impregnated with Butvar B98. Preparing the skull was difficult as the bone was softer in places than the matrix and the latter tended to remove a layer of bone as it was chipped away with an automatic mallet. Much of the matrix on the ventral surface of the skull roof has been left as a reinforcing agent as the bone is extremely thin.

Slight dorsoventral crushing has forced the anterolateral margins of the skull outwards (Plate XIV) and has caused a little warping in the occipital region, but on the whole the skull is well preserved.

Typical labyrinthodont ornament is present on all the skull roofing bones and the sensory canals where present are well impressed into this. The ornament is more reticular than that found in *B. laticeps* but is linear towards the edges of the bones, especially the squamosal and quadratojugal. So the suggestion by Bystrow (1935) that brachyopids have no regions of elongation in the skull does not apply to this deep cheek region where the pattern of ornament shows that the skull bones have grown rapidly ventrally. Watson (1956) notes this transverse elongation in the cheek region of *Batrachosuchus*, as did Säve-Söderbergh (1937) in brachyopids in general.

Dorsal Surface. In dorsal view the skull is very similar in shape to that of *Brachyops laticeps* except that less of the occiput is exposed. The orbits and choanae are rounded and the parietal foramen is small and set well back in the skull. A cross-section of the midline of the skull roof shows a strongly developed ventrally produced ridge which runs along the midline from the anterior part of the frontal bones posteriorly to end behind the parietal foramen (Fig. 1, x–y). Nine millimetres in front of this foramen the ridge divides into two, bypasses the foramen, and comes together again at the level of the ventral surface of the skull roof 6 mm. behind the foramen. The result is an elongate pineal cavity which is loaf-shaped at the level of the external opening.

The premaxillae, nasals, frontals, parietals, postparietals, postfrontals, postorbitals, supratemporals and squamosals are very like those of *Brachyops laticeps* except that the suture between the frontals and parietals is more towards the front of the skull in *B. allos*. A flange of the nasal bone which extends lateral to the external naris on each side could be a septomaxilla as shown by Shishkin (1966) in *Batrachosuchus lacer*, but no nasal-septomaxillary suture is visible. More probably the circle of bone which floors the nostril is the septomaxilla, as could have been the case in *Hadrokkosaurus* (Welles and Estes, 1969). No suture can be found between the maxillary and prefrontal bones; the suture shown in this position in Fig. 1 is hypothetical and has been placed in its most likely position in relation to the ornament and the sensory canals. If it is correctly placed it excludes the maxilla from the orbit. A thin process of the jugal extends around the anterior border of the orbit to a greater extent than it does in other brachyopids. Much of the right quadratojugal remains and forms the posterolateral corner of the skull, sending sheets of bone medially to cover parts of the posterior and anterior faces of the quadrate.

Ventral Surface. A ventral view of the skull shows unusually wide interpterygoid vacuities and an enlarged anterior palatal vacuity. The latter is tripartite (Fig. 2), as is the one found by Shishkin (1966) in *Batrachosuchus*.

Large tusks and tusk replacement pits are found in the vomers palatines and right ectopterygoid, which also bears a palatal tooth. While no palatal teeth can be found on the vomer, an additional small tusk is present right of the midline just posterior to the anterior palatal vacuity. A raised median area on the cultriform process of the parasphenoid bears a shagreen of minute denticles which are not present elsewhere on the palate.

Premaxillary, maxillary, vomer and palatine bones vary little from the characteristic brachyopid pattern as seen in *B. laticeps*. The parasphenoid body

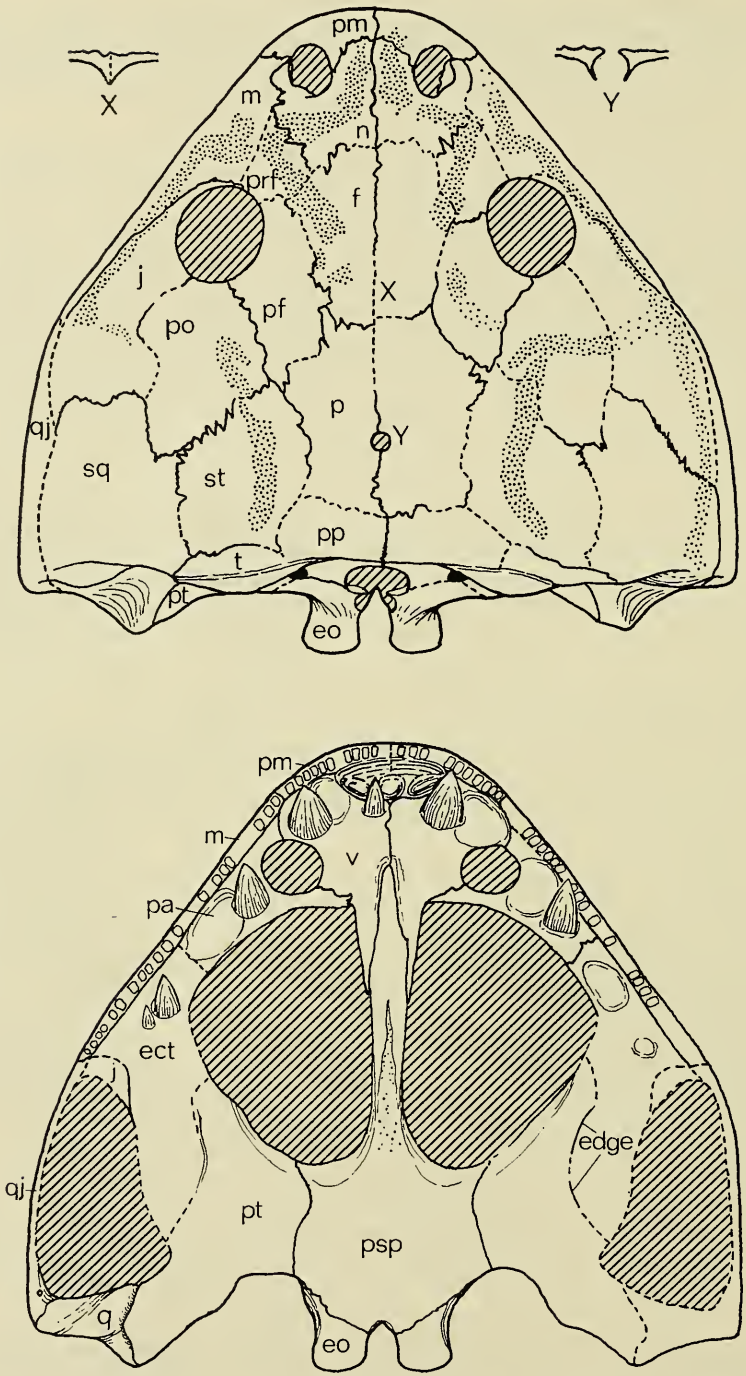

Fig. 1. *Brachyops allos* n.sp. a : Dorsal view of the skull drawn normal to the skull roof. b : Ventral view of the skull drawn normal to the parasphenoid. x, y : Sections of the skull midline at x and y. $\times \frac{2}{3}$. Sensory grooves are stippled.

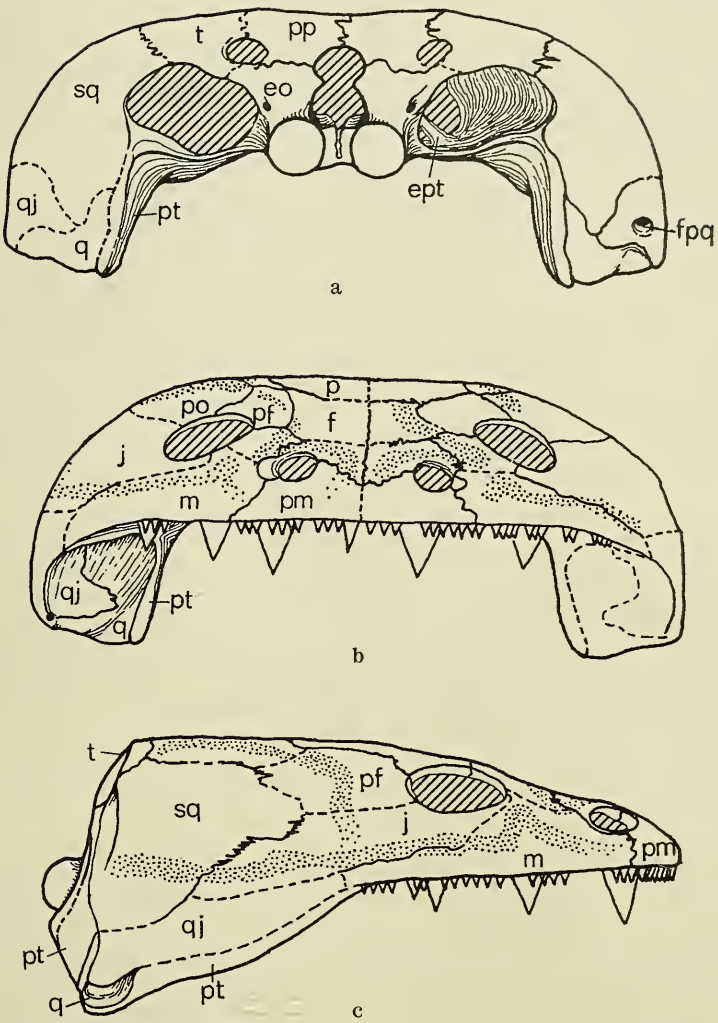

Fig. 2. *Brachyops allos* n.sp. a : Occipital view of the skull. b : Anterior view of the skull. c : Lateral view of the skull drawn normal to the saggital plane of the skull. $\times \frac{2}{3}$.

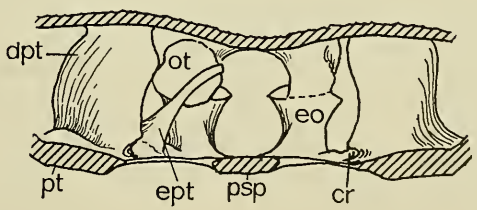

Fig. 3. *Brachyops allos* n.sp. Sketch of a section of the skull in the braincase area to show the (?) epipterygoid. Looking posteriorly from the proximal end of the cultiform process. $\times \frac{2}{3}$

is arched a little dorsally and extends further posteriorly than it does in *B. laticeps*, so that the exoccipitals are separated in the midline. No crista muscularis as noted by Welles and Estes in *Hadrokkosaurus* is present, but a well-developed ridge runs from the cultriform process behind the interpterygoid vacuity and is continued on the palatal ramus of the pterygoid. The cultriform process dips dorsally above the vomers at its anterior end but is narrower here than it is in *B. laticeps*, being clasped laterally by posterior extensions of the vomers rather than bearing these on its ventral surface.

The pterygoids are typically brachyopid except in their lateral margins. On the left side the anterolateral border of the palatal ramus of the pterygoid is a true edge (edge, Fig. 2), so that on this side the ramus is less than half the width of the right ramus. However, a ridge on the right ramus follows a similar line to that taken by the true edge of the left ramus. I interpret this edge as being the suture line between the pterygoid and ectopterygoid, so that the ectopterygoid extends posterolaterally along the pterygoid.

The right quadrate is preserved and shows an advanced level of ossification when compared with other brachyopids. The condyle has a lateral area and a larger and more ventral median area, the two being linked by a groove to form a screw-shaped condyle similar to that found in other well ossified rhachitomes.

Because of the greater degree of ossification in this specimen, an occipital view differs from the same view in other brachyopids in that the gap between the squamosal-quadratojugal complex and the pterygoid is filled with a dorsal extension of the quadrate. The supraoccipital and basioccipital areas are unossified, but a well-developed processus lamellosus divides the supraoccipital space from the foramen magnum. The processus basalis of the exoccipital is even more fully ossified than it is in *Hadrokkosaurus*. A paraquadrate foramen is present in the right quadratojugal. The posterior face of each tabular has a large rugosity above the paroccipital process.

The lamina ascendens or dorsal process of the pterygoid is much the same as the one present in *Hadrokkosaurus* except that it reaches the skull roof, touching the tabular medially and the squamosal more laterally.

Epipterygoid. On the right side, 4 mm. medial to and a little behind the leading edge of the dorsal process of the pterygoid, is a further ossification (Figs 2 (*a*), 3) which may be an epipterygoid. This originates from an 8 mm. base on the pterygoid near its suture with the parasphenoid and ascends dorsomedially, becoming narrower and rounder to end just anterior to the postparietals and 7 mm. lateral to the midline. A small excavation beneath the anteromedial edge of the ascending process of the pterygoid is probably the conical recess for the basipterygoid process of the basisphenoid. Between the head of the (?) epipterygoid and the anterior face of the paroccipital process and attached to the latter is an irregular ossification which may be part of the otic capsule.

From *Eusthenopteron* through early amphibia like *Eryops* and *Edops* and later Triassic Amphibia like *Parotosaurus* the epipterygoid whether more or less well ossified bears a contant relationship to the pterygoid ; it is found adpressed to the lateral (morphologically internal) surface of the dorsal process of the pterygoid. In *Eusthenopteron* and early Amphibia the palatoquadrate cartilage is present as a continuous element which runs forward from the quadrate along the dorsolateral margin of the pterygoid, but is usually not preserved anterior of the epipterygoid region. In the more " advanced " labyrinthodonts ossification in the palatoquadrate is gradually reduced to a quadrate element and an epipterygoid element, the latter consisting of an expanded basal portion which usually forms the dorsal roof of the conical recess for the basipterygoid process of the basisphenoid, an anterodorsal process which eventually becomes the columella cranii of reptiles, and a posterodorsal or otic process. In Triassic

amphibians such as *Lyrocephalus*, *Parotosaurus* and *Metoposaurus* the otic process is lost. In life, no doubt a cartilaginous connection was maintained between the quadrate and the epipterygoid.

Previously described brachyopids have been poorly ossified, a condition reflected in their fragmentary or missing quadrates and the lack of any ossification in the braincase area. In *Brachyops allos* the quadrate is better ossified than it is in many earlier labyrinthodonts, and it would not be unreasonable to expect some part of the epipterygoid to be preserved. However, the column of bone preserved in *B. allos* differs from other known epipterygoids in that its foot lies just medial to the pterygoid rather than being adpressed to its lateral edge, so that any cartilaginous connection between the epipterygoids and the quadrate would be extremely awkward.

One possibility is that the element is a displaced stapes, but Watson described a very different stapes in *Batrachosuchus*, as did Bystrow (1937) in *Dvinosaurus*. Also, the bone is apparently in place within the skull and slopes dorsomedially ; a stapes would be more likely to have its distal end at least outside the skull, and would slope dorsolaterally.

Relationships of *Brachyops allos*

In their review of the brachyopids Welles and Estes (1969) used the method developed by Welles and Cosgriff (1965) for their review of the capitosaurus. A series of arbitrary measurements is made on the skulls, and indices are derived from these measurements. The sum of the differences between indices for any two species is then assumed to be a useful indication of the relationship between these species. Welles and Estes acknowledge the various shortcomings of this method of analysis, one of which is the small number of specimens from which all measurements can be obtained. Data from additional specimens can only improve this situaton so the relevant figures for *B. allos* are tabled below.

The figures given are for the reconstructed skull ; they differ slightly from those obtained from the actual specimen.

	cm.
Interorbital breadth, A	4·5
Breadth of skull roof across quadratojugals, B	14·2
Midline postorbital length, D	5·6
Length of vomers, E	2·1
Midline distance between nostrils and orbits, F	1·6
Breadth across vomers, G	2·7
Height of parasphenoid, H	2·4
Internarial breadth, J	1·6
Length of skull roof, L	11·0
Midline preorbital length, O	3·3
Distance behind orbits of parietal foramen, P	3·0
Length of body of pterygoid, Q	2·3
Breadth across pterygoids at concavity, R	8·5
Distance of parietal foramen in front of end skull table, T	2·2
Midline orbital length, U	2·0
Length of interpterygoid vacuity, Y	5·25
Breadth of interpterygoid vacuity, Z	3·7

Indices :

B : L	130	U : L	19	G : E	129
J : L	15	D : L	51	Q : R	27
A : L	41	P : A	66	Y : L	48
O : L	30	T : A	49	Z : Y	70

Sums of Differences (using Welles and Estes data as plotted in figs 2-13):

Brachyops allos / *Hadrokkosaurus bradyi*	149
Brachyops allos / *Batrachosuchus watsoni*	73
Brachyops allos / *Batrachosuchus browni*	61
Brachyops allos / *Brachyops laticeps*	62
Brachyops laticeps / *Blinasaurus henwoodi*	146
Brachyops allos / *Bothriceps major*	101
Brachyops allos / *Bothriceps australis*	113
Brachyops allos / *Dvinosaurus primus*	155

Assuming that the smaller totals of index differences are real measures of relationship, this table shows that *Brachyops* is most closely related to *Batrachosuchus* and next to *Bothriceps*—the same finding as Welles and Estes' original analysis showed. The fact that *Brachyops allos* is closer by one point to *Batrachosuchus browni* than to *Brachyops laticeps* only emphasizes the fact that until more brachyopid specimens are known a few points difference between two skulls cannot be taken as a significant measure of a relationship or a non-relationship; the equivalent figures for the *Brachyops allos* skull before reconstruction indicate that *B. allos* is closer by five points to *B. laticeps* than it is to *Batrachosuchus watsoni*.

Welles and Estes suggest that a sum of differences of 57 might reasonably be considered as representing a specific level. If this is so, then *Brachyops allos* should be placed in a genus separate from *Brachyops laticeps* and *Batrachosuchus*. This would be " splitting " in the extreme and it could be more valid to unite *Brachyops laticens*, *Brachyops allos* and *Batrachosuchus* into a single genus.

Whether it is *Brachyops* or *Batrachosuchus*, *Brachyops allos* will link Welles and Estes' two Palaeogeographic units, their Australian brachyopid line, and their second brachyopid line which includes African and Indian-North American forms.

Brachyops allos is thus a particularly well-preserved and well-ossified member of its family and hence shows several features not previously found in the Brachyopidae. These include the presence of a paraquadrate foramen, an area of denticles on the parasphenoid, an ossified quadrate and a probable epipterygoid.

Being the first brachyopid to be described since Welles and Estes' analysis of the family, it can be used to test their methods. These proved to be accurate in indicating relationships at a level a little above the generic one, but, at least until the discovery of more specimens allows a statistically valid index to be calculated, the methods cannot be used to establish generic or specific relationships.

Acknowledgements

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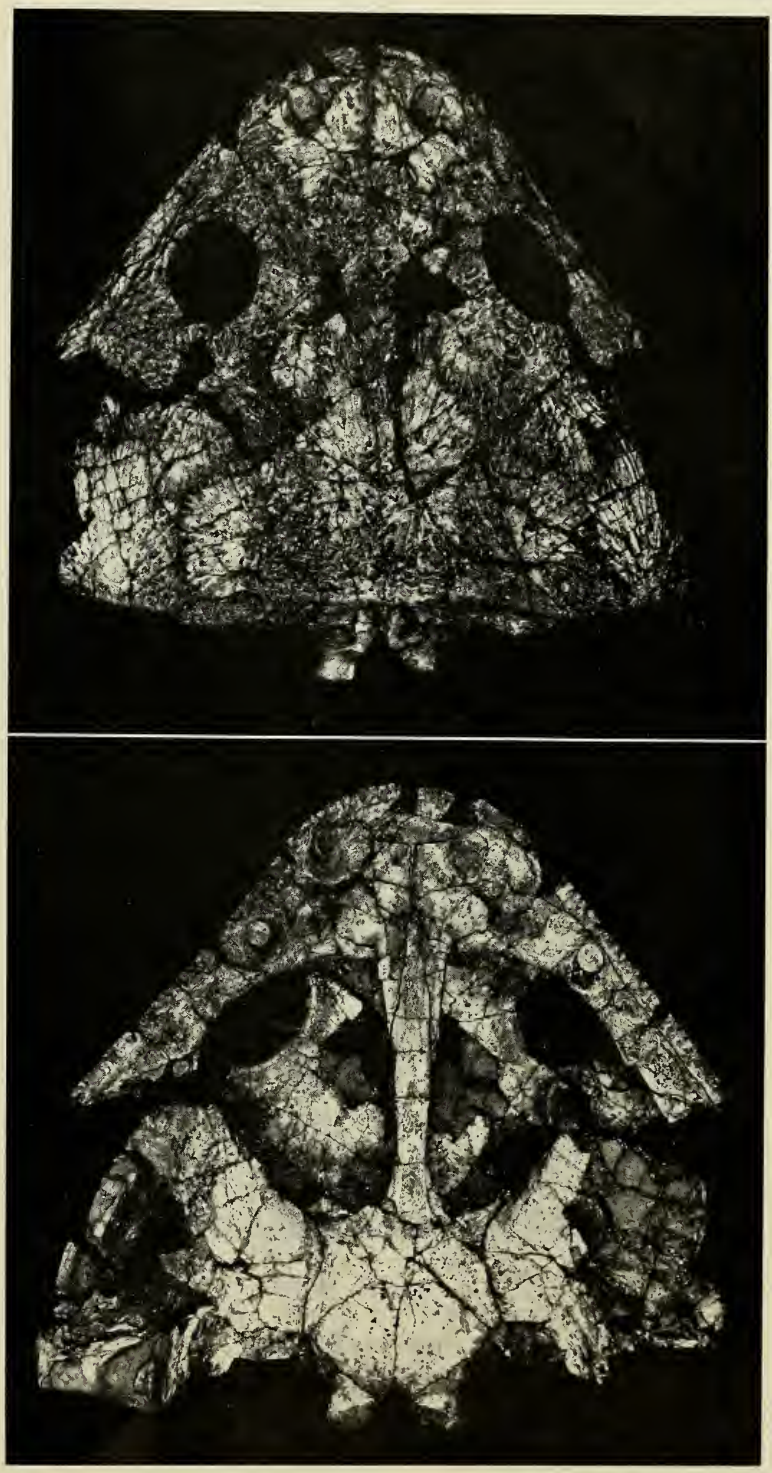

Brachyops allos n.sp. a : Dorsal view of the skull. b : Ventral view of the skull. $\times \frac{2}{3}$.